

AN ABERRANT, TWINNED PREMOLAR IN EARLY
EOCENE *HYOPSODUS* (MAMMALIA: CONDYLARTHRA)

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ABSTRACT

A recently discovered partial skull of *Hyopsodus* contains a highly deformed right upper fourth premolar. Crown morphology and occlusal relationships indicate this is a single, geminated tooth, formed from an aberrantly split tooth bud early in ontogenetic development. The premolar appears as labial and lingual mirror images that share a centrally placed paracone. Morphogenic fields acting on the twinned premolar primordia are hypothesized as a possible explanation for the abnormal morphology.

INTRODUCTION

Abnormal tooth morphology has been reported for a variety of mammalian fossil taxa (e.g. McKenna, 1960a; Rose and Smith, 1979; Lucas and Schoch, 1987). Although papers addressing dental ontogeny and pathology have been numerous (more recent examples include Butler, 1967; Pindborg, 1970; Archer, 1975; papers in Kurten, 1982; Roth, 1989), there has been no broad treatment of anomalous dentitions for many extant and fossil groups. This is almost certainly partly attributable to the infrequency with which specimens displaying these anomalies are reported in the literature. Described here is an unusual upper fourth premolar of *Hyopsodus* (Mammalia, Condylarthra) recently discovered in the collections of The Carnegie Museum of Natural History (CM).

DESCRIPTION

CM 6428 (Fig. 1) is a partial skull including right and left P3-M3. The left P2 is crushed and incomplete. The anomalous tooth is the right fourth premolar. The specimen label indicates it was collected "North of Elk Creek, three miles south of Basin, Wyoming" in the Bighorn Basin. A lack of precise stratigraphic information precludes assigning this specimen to a more precise biostratigraphic age than Graybullian (early Wasatchian, early Eocene). The skull is preserved within a hard, grey claystone matrix containing a small number of reddish oxidized nodules. In addition to the dentition, CM 6428 preserves fragmentary pieces of the maxilla, frontal bone and the left maxillary and malar zygoma. Ventrally, most of the palate is not present with the exception of a small surface of broken palatine bone situated posterior and medial to the left M3.

No species identification of CM 6428 is made here. The molar morphology is similar to that in *Hyopsodus loomisi* (McKenna, 1960b) and Bown's (1979) *Hyopsodus*, sp. nov., and shares the following characters with these taxa: small size; hypocone absent from the posterior shelf of M3; poorly developed ectocingula on all upper molars; hypocone somewhat weakly expressed on M1 and M2.

The pathologically developed right P4 is nearly unworn. In normal *Hyopsodus*,

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Fig. 1.—CM 6428. Partial skull of *Hyopsodus*, preserving upper RP3–M3 and fragmentary LP2, LP3–M3. The arrow points to the deformed RP4.

P4 is a subtriangular tooth (transverse width greater than anteroposterior length) featuring a prominent conical labial cusp, the paracone. A short loph runs anterior from the paracone to a distinct, variably strong parastyle. A postparacrista sharply descends posteriorly from the paracone to the posterior cingulum where a small cusp, frequently labelled the metacone, is present. Lingually, there is a crescentic protocone, the apex of which is usually anterior to the transverse midline of the tooth. The wings of the protocone crescent descend from its tip labially where they wrap around the anterior and posterior margins of the base of the paracone. Generally, the posterior cingulum is more prominent and shelf-like than the anterior cingulum. Premolars of Graybullian species of *Hyopsodus* usually have more poorly developed external cingula than stratigraphically younger *Hyopsodus* (Gazin, 1968).

The right P4 (left P4 is not aberrant) of CM 6428 differs greatly from the typical morphology (Fig. 2). On the external margin, a relatively large crescentic cusp protrudes labially, forming a shelf which is basined at its center. Its appearance



Fig. 2.—CM 6428, right maxilla. Occlusal view of upper RP3, pathologic RP4, RM1–3.

is suggestive of an auxiliary protocone labial to the paracone and crista—a mirror image of its normal lingual position. Immediately lingual to this crescentic cusp and central on the crown is a tall paracone, featuring anterior and posterior crista that split and diverge as they descend towards the lateral margins of the tooth. In occlusal view these crests form an X-shape, with the apex of the paracone at the juncture. A crack runs anteroposteriorly across the widest portion of the crown and bisects the “X” configuration of the cristae. The two crests that extend anteriorly from the paracone end in well-developed cusps, whereas the posterior cristae broaden to less developed cusp-like structures at their ends. Since a strong resemblance exists between the labial and lingual morphology of both the anterior paracristae and the posterior paracristae, the crown of RP4 appears as lingual and labial mirror images which share a centrally placed paracone. Given this interpretation, each of the two anterior cusps occurs in the parastyle position of a normally formed *Hyopsodus* P4, and each of the two posterior incipient cusps lies in the metacone position. The labial “parastyle and metacone” are connected to the lingually extending wings of the crescentic outer cusp. The more heavily worn lingual “parastyle and metacone” are similarly connected to a lingual protocone, which is located in its normal position. The protocone is somewhat larger than the crescentic outer cusp but is similar in shape.

Overall, the degree of lingual protocone and metacone development and the size of the lingual parastyle do not differ significantly from the normal condition. The labial cusps and the size of the trigon they form are somewhat smaller but are no more than proportionately abnormal.

Preparation at the base of right P4 reveals four roots, rather than the usual three: one each under the labial cone and protocone, and one each under the double parastyles and metacones. The latter two roots are thick and may diverge more deeply within the maxilla.

Dental wear implies that the anomalous right P4 severely affected the mastication of the *Hyopsodus* individual. The preserved dentition on the right side of the maxilla is only moderately worn, especially the anomalous P4, on which a small protocone wear facet and a flattening of the lingual paracristae are the only signs of abrasion. In contrast, the left dentition is much more heavily worn (Fig. 1); M2 and M3 display considerably larger facets and left M1 is a completely abraded and featureless tooth, with the exception of labial remnants of the paracone and metacone. Left P4 is also flattened and P3 is worn on the posterior sides of the paracone and protocone. Apparently, far more occlusal contact occurred on the left side of the animal's dentition during its lifetime. This was probably related to the abnormal occlusion caused by right P4.

DISCUSSION

Right P4 is interpreted as a twinned or geminated tooth (Tannenbaum and Alling, 1963; Levitas, 1965; Pindborg, 1970), rather than the result of crown fusion induced either by tooth germ dislocation or by the consolidation of tooth buds during early development (Pindborg, 1970; Lucas and Schoch, 1987). A geminated tooth is thought to be the product of an additional, incomplete division in a single tooth bud. The evidence supporting this conclusion includes: 1) The tooth twinning forms labial and lingual mirror images with a plane parallel to, not transverse to, the anteroposterior axis of the dental row. It is more likely that fusion with a tooth immediately anterior or posterior to P4 would produce a transverse mirror plane. The possibility that right dP4 is cemented to a normally

erupting P4 is rejected on morphologic grounds. Upper dP4 in *Hyopsodus* is a molariform tooth (Gazin, 1968). Similarly, an explanation of the labial fusion of P3 (or dP3) to P4 involves the occurrence of an unsubstantiated supernumerary P3 occupying the position anterior to the aberrant tooth. Archer (1975), however, described a divided (but not geminated) lower third premolar associated with an extra premolar in a specimen of *Dasyurus*; 2) Though an enamel crack does run roughly parallel to the mirror plane of P4, this crack cannot be regarded as sutural evidence of fusion. It appears to be jagged, caused by postmortem processes and diminishes as it ascends the paracone. The paracone itself shows minimal structural twinning or fusion at its apex; 3) Each mirror image bears a strong resemblance to a typical fourth upper permanent premolar.

The possible developmental causes of the premolar's abnormal morphology are most readily understood within the context of normal therian tooth ontogeny. The specifics of ontogenetic dental development in mammals are, as yet, still primarily descriptive. It is well established that, initially, ectodermal neural crest mesenchyme contacts the oral epithelium within the upper and lower jaws. This is followed by the appearance of the dental lamina, formation of embryonic toothbuds and the establishment of cusp pattern. These steps were described as two of three discrete stages by Kollar and Lumsden (1979) and precede a final stage characterized by dentin and enamel deposition. Presumably, most aberrant tooth morphologies, particularly in a single tooth, occur during tooth bud or cusp pattern formation (Levitas, 1965; Pindborg, 1970). This may appear to simplify matters, but unquestionably the genetic and inductive interactions are quite complex at this stage (Butler, 1982).

Cusp formation proceeds as the epithelium folds in response to mesenchyme induction. The paracone emerges as the first distinct cusp, with subsequent cusp formation occurring at specific locations marginal to the paracone (Butler, 1956, 1971). Because premolars and molars have anteroposterior and labiolingual morphologic polarity, a morphogenic field having at least these two dimensions has been proposed (Butler, 1982) as a theoretical model.

The deformed premolar in CM 6428 appears to be a single tooth. The crown is singular and does not appear to be fused. The dental formula of the specimen is normal—as far as can be detected; and the deformity is oriented labiolingually. It is suggested that gemination occurred in the tooth bud destined to form right P4. The doubling was probably not complete in that the paracone appears to be a single structure. After the appearance of the paracone, the crown morphology developed twice on the lateral margins due to the split primordia reacting individually to morphogenic fields similar to those of Butler's (1982) model. Interestingly, in this case, a paracone/protocone gradient may be inferred, rather than a more general labiolingual gradient, supporting a primary organizational role for the tissue involved in paracone formation. Crown morphology is arranged around this cusp, which is centrally, rather than labially, located in the CM specimen. Any possible anteroposterior field seems to have been unaffected since none of the abnormalities appear to follow an anterior-posterior pattern.

Inbred populations of mammals appear to exhibit a high frequency of dental abnormalities (Archer, 1975). Few studies exist, however, that document the distribution of tooth pathologies among non-domesticated mammals. Recently, it has been suggested that there existed a lower frequency of skeletal pathologies among early Cenozoic mammals than exist today among Recent taxa (Lucas and Schoch, 1987). Without additional reports and integrated studies of current and

fossil dental abnormalities, this conclusion is far too simplistic. Unpublished investigations of Wasatchian and Bridgerian *Hyopsodus* document a large number of individuals with accessory and twinned cusps that may indicate other types of ontogenetic disturbance.

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